

The University of Chicago

AN ECOLOGICAL STUDY OF SOME
ORTHOPTERA OF THE
CHICAGO AREA

A PART OF A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

1936

By

H. F. STROHECKER

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INTRODUCTION ¹

The geographical and local distribution of North American Orthoptera has received the attention of a number of capable workers. Morse ('99) demonstrated a general correlation of the distribution of New England locusts with mean annual isotherms. His conclusion (p. 320) was that the delimitation of range is "... distinctly climatal in character, although strongly influenced by physiography and its attendant conditions."

Collecting and field observations during the past three years have demonstrated an ecological succession of Orthoptera corresponding in a general way to the plant succession on the sand dunes along the southern shore of Lake Michigan. This region has been the object of ecological study since the pioneering work of Cowles in 1899. It has been hoped that a comparison of the local distribution of the species of Orthoptera with the summarized data on vegetation and the character of the physical environment in the stages of the plant succession might shed some light on the specific factors operative in the limitation of range of certain species of Orthoptera.

HISTORICAL

The species of Orthoptera occurring in Illinois and neighboring states have been treated by Thomas ('76, '80), Blatchley ('03, '20), Hancock ('11) and Hebard ('34). These works, especially those of Blatchley and Hancock, contain many notes on the gross features of the habitats of particular species.

References to Illinois and Indiana Orthoptera are to be found in many ecological papers, especially those of Hart and Gleason ('07), Shelford ('13) and Vestal ('13).

PHYSIOGRAPHY

A rather full description of the physiographical features of the region about Chicago is contained in Cowles' ('99, '01) accounts. Along the southern and southeastern shores of Lake Michigan sand deposition and wind

¹From ecological studies under the supervision of Dr. W. C. Allee. I wish also to acknowledge indebtedness to Dr. Henry Fox and Mr. M. Hebard, who gave opinions in some cases of doubtful identity of specimens of Orthoptera. Drs. G. D. Fuller and C. E. Olmsted have been of indispensable assistance in the identification of plants.

action have produced dunes of considerable height and extent; the greatest elevation is about two hundred feet above lake level. The southwestern shore of Lake Michigan lacks sand dunes of any size but many of the vegetational features are the same, particularly as regards grasses and other herbaceous plants.

The localities west of Chicago at which collecting was done, Palos Park and the Pilcher Arboretum near Joliet, lie on the Valparaiso moraine. The soil is a heavy black clay of glacial deposition. At Palos Park the usual type of forest is composed of mixed oaks or oak and hickory. That part of the Pilcher Arboretum which was visited is a forest of sugar maple, regarded as the forest climax on this soil as well as on the sand soil of the dunes.

The forest at Smith, Indiana, is on a clay soil which was covered by a deposit of sand a foot or two in depth, presumably during the Glenwood stage of Lake Chicago. The drainage is poor; part of the forest floor is sometimes under water during spring. Of the other climax forests which will be referred to that at Lakeside, Michigan, is on sandy clay while the same type of forest at Saugatuck, Michigan, is developed on the sand dunes. The necessity for considering these separately will be disclosed in the description of the vegetation and of the distribution of Orthoptera.

VEGETATION AND ORTHOPTERA

The associates recognized in the following description are those of Cowles' ('01) schematization of the ecological succession of plants in the Chicago area. Since the Orthoptera are closely associated with vegetation the most abundant and characteristic plant species of each associates will be indicated, with especial attention to those upon which these insects have been observed to feed. Fuller ('25) has prepared species lists and compact descriptions of the plant communities of the Chicago region.

1. *The Beach*. This early stage of the succession is devoid of plants except for occasional specimens of *Cakile* and *Artemisia*. While the physical factors such as light intensity, evaporation, etc., are undoubtedly similar to those of the next associates the practical absence of plants precludes the establishment of Orthoptera. Stray specimens of *Trimerotropis maritima interior* are to be found but no significance can be attached to their presence.

2. *The Foredune* consists of low mounds of sand from five to fifteen feet high. The dominant plant of this associates is the Marram grass, *Ammophila arenaria* Link. *Calamovilfa* also grows here and there are extensive stands of the sand cherry, *Prunus pumila* L.

Associated with the grasses are *Trimerotropis maritima interior* E. M. Walker, here approaching its western limits of distribution, *Psinidia fenestralis* Serv., and *Ageneotettix deorum* Scud. The last named is not common on the southern shore of Lake Michigan but is very abundant on the dunes at Waukegan, Illinois, which is on the western shore of the lake just north of

TABLE I. The distribution of orthoptera in the associates of the forest succession in the Chicago area

	Foredune	Poplar	Pine	Black oak on sand	Oak-hickory on clay	Climax, Smith, Ind.	Climax, Joliet, Ill.	Climax, Lakeside, Mich.
Blattidae								
<i>Parcoblatta pennsylvanica</i> (DeGeer).....	—	—	*	*	*	*	*	*
<i>Parcoblatta uhleriana</i> (Saussure).....	—	—	—	—	*	*	—	—
<i>Parcoblatta virginica</i> (Brunner).....	—	—	—	*	*	*	—	—
Phasmidae								
<i>Diapheromera femorata</i> (Say).....	—	—	—	*	*	*	*	—
<i>Diapheromera blatchleyi</i> (Caudell).....	—	—	—	*	*	—	—	—
Acridiidae								
<i>Tettigidea lateralis parvipennis</i> (Harris)....	—	—	*	*	*	*	*	—
<i>Chloealtis conspersa</i> (Harris).....	—	—	—	*	*	*	—	—
<i>Ageneotettix deorum</i> (Scudder).....	*	*	*	—	—	—	—	—
<i>Trimerotropis maritima interior</i> (E. M. Walker).....	*	*	—	—	—	—	—	—
<i>Psinidia fenestralis</i> (Serv.).....	*	*	*	—	—	—	—	—
<i>Spharagemon collare</i> (Scud.).....	*	*	*	—	—	—	—	—
<i>Spharagemon bolli</i> (Scud.).....	—	—	—	*	*	—	—	—
<i>Arphia sulphurea</i> (Fabricius).....	—	—	*	*	*	—	—	—
<i>Melanoplus flavidus</i> (Scud.).....	*	*	*	—	—	—	—	—
<i>Melanoplus angustipennis</i> (Dodge).....	*	*	*	—	—	—	—	—
<i>Melanoplus m. mexicanus</i> (Saussure).....	*	*	*	—	—	—	—	—
<i>Melanoplus keeleri luridus</i> (Dodge).....	—	—	—	*	*	—	—	—
<i>Melanoplus fasciatus</i> (F. Walker).....	—	—	—	*	*	—	—	—
<i>Melanoplus gracilis</i> (Brunner).....	—	—	—	—	*	—	—	—
<i>Melanoplus viridipes</i> (Scud.).....	—	—	—	—	*	—	*	—
<i>Melanoplus walshii</i> (Scud.).....	—	—	—	*	*	*	*	—
<i>Melanoplus punctulatus</i> (Scud.).....	—	—	—	—	*	—	*	—
<i>Melanoplus scudderi</i> (Uhler).....	—	—	—	*	*	—	—	—
<i>Shistocerca alutacea</i> (Harris).....	—	—	—	*	—	—	—	—
<i>Phoetaliotes nebrascensis</i> (Thomas).....	—	—	*	—	—	—	—	—
<i>Hesperotettix viridis pratensis</i> (Scud.).....	—	—	*	—	—	—	—	—
Tettigoniidae								
<i>Scudderia furcata</i> (Brunner).....	—	—	—	*	*	*	*	—
<i>Scudderia curvicauda</i> (DeGeer).....	—	—	—	*	*	—	—	—
<i>Amblycorypha rotundifolia</i> (Scud.).....	—	—	—	*	*	*	*	—
<i>Amblycorypha oblongifolia</i> (DeGeer).....	—	—	—	—	*	*	*	—
<i>Pterophylla camellifolia</i> (Fabr.).....	—	—	—	* ²	*	*	*	*
<i>Atlanticus testaceus</i> (Scud.).....	—	—	—	—	*	—	—	—
<i>Orchelimum sylvaticum</i> (McNeill).....	—	—	—	—	—	—	*	—
<i>Conocephalus saltans</i> (Scud.).....	—	—	*	—	—	—	—	—
<i>Conocephalus nemoralis</i> (Scud.).....	—	—	—	—	*	—	*	—
<i>Ceuthophilus</i> sp. nymphs.....	—	—	—	*	?	?	?	?
<i>Ceuthophilus brevipes</i> (Scud.).....	—	—	—	—	*	*	*	*
<i>Ceuthophilus maculatus</i> (Harris).....	—	—	—	—	*	—	—	*
<i>Ceuthophilus latens</i> (Scud.).....	—	—	—	—	*	*	*	*
<i>Ceuthophilus divergens</i> (Scud.).....	—	—	—	—	—	*	*	*
Gryllidae								
<i>Gryllus assimilis</i> (Fabr.).....	—	—	*	*	*	*	*	—
<i>Nemobius fasciatus</i> (DeGeer).....	—	—	*	*	*	*	*	—
<i>Nemobius maculatus</i> (Blatchley).....	—	—	—	*	*	*	*	—
<i>Nemobius carolinus</i> (Scud.).....	—	—	—	*	*	*	*	—
<i>Nemobius confusus</i> (Blatchley).....	—	—	—	—	—	*	*	—
<i>Oecanthus angustipennis</i> (Fitch).....	—	—	—	*	*	*	—	—

² Report of A. E. Emerson.

Chicago. It reaches its eastern limits of distribution in northwestern Indiana. *Melanoplus flavidus* Scud., *M. angustipennis* Dodge and *M. mexicanus* Sauss. are also of regular occurrence on the foredune. Northwestern Indiana marks the eastern limits of distribution of the first two of these.

While not so abundant as in later stages of the succession *Spharagemon collare* Scud. may be considered characteristic of the foredune. *Diapheromera femorata* Say has been taken occasionally on the sand cherry. In these instances the growths of *Prunus* were near stands of oak (Dune Park, Ind.). These few records do not suffice to establish it as a regular inhabitant of the foredune associates but serve to exemplify the pitfalls of ecological studies based on general collecting of animals with which one is unfamiliar.

3. *The Poplar or Cottonwood Associates.* The most conspicuous and the dominant plants of this community are the species of *Populus*, chiefly *deltoides* Marsh. Of significance to the Orthoptera are *Ammophila* and *Calamovilfa*, which persist from the earlier stage.

No species of Orthoptera are peculiar to the poplar associates nor is it characterized by the absence of any of the species occurring on the foredune. *Trimerotropis m. interior* is present in smaller numbers than on the foredune. The other foredune species are all to be found here. *S. collare* and *P. fenestralis* are somewhat commoner than in the preceding associates.

4. *The Pine Associates* is dominated by *Pinus banksiana* Lamb. This community develops only in sites protected from strong winds by dunes and is usually at some distance from the lake. The intensity of the physical factors operative is thus not altogether a direct result of modification by vegetation.

Conspicuous among the plants of the floor is the bearberry, *Arctostaphylos uva-ursi* Spreng., which forms considerable mats. The grass, *Andropogon scoparius* Michx., grows in scattered but numerous tufts in the unshaded parts of the community. Several species of *Vitis* are abundant.

As in the case of the poplar associates the pine community has no species of Orthoptera characteristic of it alone unless we so regard the three species *Hesperotettix viridis pratensis* Scud., *Phoetaliotes nebrascensis* Thomas and *Conocephalus saltans* Scud., which, however, are more typical of sand prairie and have been taken from among growths of pine at only one locality. They were found in the bunches of *Andropogon* and in the mats of *Arctostaphylos*. Of the Orthoptera found in the earlier associates all persist in the pine except *T. m. interior*. *M. angustipennis* apparently reaches its height of abundance in this stage of the succession.

Several species characteristic of the next successional stage are to be found at times in the pine community. *Arphia sulphurea* Fabr. is present in the adult stage until late May. *Gryllus assimilis* Fabr., *Nemobius fasciatus* DeGeer and *Tettigidea lateralis parvipennis* Harris, while not found during the summer, appear to invade the pine associates in September. *Parcoblatta pennsylvanica* DeGeer evidently moves into the pine associates nightly. Great numbers of unhatched and shriveled oothecae of this cockroach have been found

under the bark of pine logs. Hibernating nymphs of this species are also to be found in the pine community in October and November.

5. *The Black Oak Associates*. As the name indicates, the dominant plant of this community is *Quercus velutina* Lam. There is a fairly evenly distributed and abundant undergrowth composed of many species of shrubs, common among which are *Ceanothus*, *Gaylussacia*, *Vaccinium* and *Vitis*. Where the shade is not too heavy several grasses and sedges, *Panicum*, *Stipa*, *Aristida* and *Carex* grow on the forest floor.

The transition from pine to oak forest marks a rather abrupt change in the characteristic Orthoptera. While, as noted above, several species range from the oak into the pine associates these are by no means of universal or constant occurrence in the latter. Whereas the four earlier associates have several species in common, some of which range from pine to foredune, the oak forest possesses a distinctive fauna of Orthoptera. Apparently first in the colonization of the oak forest are *A. sulphurea* Fabr., *Spharagemon bolli* Scud., *Shistocerca alutacea* Harris and *Melanoplus keeleri luridus* Dodge. *M. fasciatus* Walker, *M. walshii* Scud. and *Chloealtis conspersa* Harris are of discontinuous distribution in the black oak forest. *M. dawsoni* Scud. has been found in numbers in the scrubby growths of oak on the western shore of the lake. It reaches its southern limit of distribution in this longitude at Waukegan, Illinois, about thirty miles north of Chicago. Four species of Tettigoniidae and five of Gryllidae occur regularly in the black oak forest. There are two species of phasmids and two cockroaches. Table I indicates the species of Orthoptera found in the black oak forest on sand.

6. *The Red Oak-White Oak Associates* is not markedly different from the preceding in the herbaceous flora of the floor; such plants as *Panicum*, *Carex* and *Ceanothus* are found in both types of forest. Neither does there appear to be any conspicuous difference in the species of Orthoptera found in all the oak associates as they occur upon sand.

A similar forest is developed upon the clay west of the city of Chicago. A study of the Orthoptera in such a forest at Palos Park, Illinois, reveals that all the species characteristic of the oak forest on sand are present with the exception of *S. alutacea*. *M. keeleri luridus*, *S. bolli* and *A. sulphurea* are typical of the mixed oak-hickory forest on clay, being most abundant in the peripheral parts of the forest. To these are added *Atlanticus testaceus* Scud. and *Melanoplus viridipes* Scud. It is impossible to separate clearly the black oak from the red oak-white oak-hickory associates on the basis of the Orthoptera found in them. All the species listed (table I) are not to be found at any one locality but the association of certain species is not constant enough to enable recognition of definite successional stages indicated by the dominant trees. The one exception to this is the case of small, rather isolated tracts of black oak such as may be seen at Ogden Dunes, Ind. Here one encounters only the fully winged species which occur in the oak forests. This may be dependent merely upon the ability of these species to reach such isolated habi-

tats while the dissemination of the wingless types must be, of necessity, slower and through more continuous habitats. The increase in number of species in the oak-hickory forest on clay as compared with the oak forest on sand is probably, as will be pointed out, not due to differences in vegetation.

7. *The Subclimax Community* is not well exemplified in the Chicago region unless we accept the oak-hickory forest on clay as representative of this stage. A good development of this phase of the forest succession as it occurs upon sand is to be seen at Lakeside, Michigan. The transition from oak to subclimax forest is indicated by the establishment of such trees as *Acer*, *Fagus* and *Tilia*, and by the decrease in the amount of herbaceous vegetation.

The subclimax on sand at Lakeside has not been well studied due to its distance from Chicago. A few species of Orthoptera have been taken here, *Parcoblatta pennsylvanica* DeGeer, *P. virginica* Brunner, *P. uhleriana* Sauss., *M. viridipes* Scud. and *Ceuthophilus divergens* (Scud.). This stage of the forest succession is not included in table I because of the paucity of data concerning it. It appears, however, that the Orthoptera represented in this associes are also characteristic of both earlier and later stages.

8. *The Climax Forest* eastward from Chicago is dominated by *Acer saccharum* Marsh. and *Fagus grandifolia* Ehrh. On the eastern shore of Lake Michigan at Saugatuck the hemlock forms a prominent part of the climax forest. West of Chicago the beech and hemlock do not occur and as a result the climax forest is an almost pure stand of sugar maple.

As regards both the herbaceous flora and the Orthoptera, the climax forest must be considered in two aspects. Where open spaces occur due to road-making or selective lumbering as at Smith, Indiana, and in the Pilcher Arboretum at Joliet, Illinois, considerable areas of the forest floor are covered by species of *Carex* and *Hystrix patula* Moench. Jewelweed, *Impatiens*, is a common herb of the climax forest. In the marginal parts and open spaces of the climax one encounters some of the species of Orthoptera typical of the earlier associes. At Smith, Indiana, along the edges of a small road through the forest, are found *M. walshii*, *C. conspersa*, *A. testaceus* and other species which occur in the oak and oak-hickory forest. These are more restricted in their distribution through the climax forest and distinctly fewer in number than in the oak or oak-hickory associes. A few specimens of *Melanoplus punctulatus* Scud. have been taken in the climax forests at Joliet and at Smith. The elongate or caudate phase of *T. lateralis parvipennis*, which is present in the oak associes, is represented in the climax by the abbreviate phase only, in which the pronotum reaches only to the tip of the abdomen.

The heavily shaded portions of the climax associes harbor only such secretive Orthoptera as *Nemobius confusus* Blatch. and a few species of *Ceuthophilus*.

The beech-maple forest at Lakeside, Michigan, represents a climax little affected by man. The leaf canopy is almost unbroken. The herbaceous flora

is limited to very few species but there is an abundant growth of the bed-straw, *Galium*.

Four species of *Ceuthophilus*, one cockroach and the katydid *Pterophylla* are known to inhabit this forest. No other Orthoptera have been taken or observed on several trips to this woods.

The distribution of the species of Orthoptera through the plant succession in the Chicago area is presented in condensed form in table I. This is not, of course, a complete species list for the region around Chicago but represents only those species encountered in the plant succession dealt with. It leaves out of account the Orthoptera found in such habitats as sphagnum bogs, prairie and stream margins.

PHYSICAL FACTORS

Quantitative determinations of various physical factors in the different stages of the forest succession have been reported by several workers from time to time. In spite of the fact that these measurements have been in most instances the summation of two or three years observations they are, as regards their usefulness in the present study, incomplete in some important respects.

1. *Evaporation*. This factor has been studied by Fuller ('12) and his students. A resumé was published by this author in 1914. He found a high rate of evaporation in the poplar associates during the summer, amounting to an average of twenty-two cc. per day. While he has published no data on this factor in the foredune associates it is probable that a similar condition prevails there. Evaporation in the pine associates is about half that in the poplar and about equal to that in the black oak community. It diminishes successively but not greatly in the other associates.

This work was done from the viewpoint of the botanist; the determinations of evaporation were made at a height of 20–25 cm. above the earth. This does not indicate exactly the conditions to which a ground-frequenting insect would be subjected. It is, however, only in the case of the pine associates that the data given seem insufficient for the purpose of the present article.

The pine community is one where stress of physical factors is sharply delimited. Fuller's measurements were made in sites shaded through the greater part of the day. Fully three-fourths of the area of the complex called pine associates is subjected to full solar radiation through much of the day. Hence the data of Fuller do not answer the question of evaporation rates in exposed sites in the pine community and especially that prevailing on clear summer days when surface temperatures are very high. No further data, however, are available. Figure 1 shows the progressive decrease in the evaporating power of the air through the plant succession, with conditions in the poplar community taken as unity (22 cc. per day).

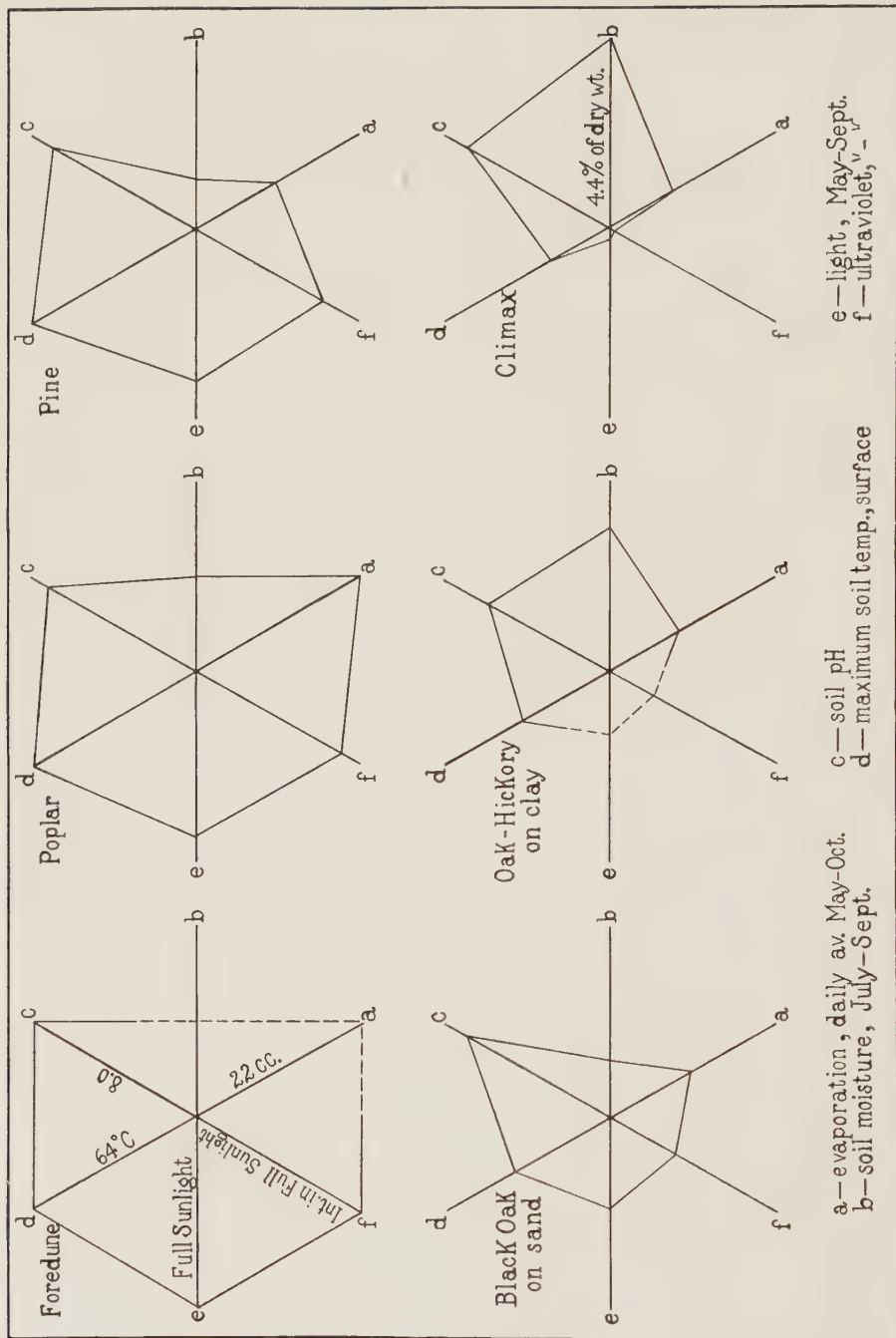


FIG. 1. Physical factors in the plant associates described. In the case of sunlight the average daily total during the period May-September 1935 was 430 G.-cal./cm.²/min. (Pyreheliometer records of meteorological station. University of Chicago.)

2. *Soil Moisture*. Fuller ('12a, '14) found the amount of growth-water to be greatest in the beech-maple forest (4.4% of dry wt.) during the summer and early autumn. This condition is taken as unity. Growth-water (that available to plants) probably represents, in general, the amount of water available to all organisms. Fuller found that a dry mulch of sand three to five cm. thick preserved the deeper water in the cottonwood associates and, due to its sparser vegetation, the amount of ground water here was greater than in the pine and black oak associates.

3. *Soil pH*. Kurz ('23) published the results of determinations of this factor. The great variation of soil pH in sites close together precludes any conclusion as to the average of this condition. This variability is most marked in the more advanced associates. Kurz reports a pH of 4.5 where wood had decayed.

The points plotted on the pH axis in Figure 1 are representative soil pH measurements in the different associates. Only the top layers of soil are considered here. From Kurz's data and discussion it appears that in the sand dunes decreasing alkalinity is due for most part to the leaching out of basic material carried in the wind-blown sand. Leaching seems to be the most important factor in the change in pH of moraine soils as the flood plains in such areas are consistently more alkaline than the hills.

The pH axis is, of course, a logarithmic device. Hence the length of these axes in the figures for the different associates is not in proportion to that of the other axes. The greatest alkalinity is found in the sand of the fore-dune (pH 8.0). This is gradually reduced to neutrality (pH 7.0) or, in some sites in the pine associates, to slight acidity (pH 6.0). From Kurz's data it appears that neutrality is the most common condition of the soils of the pine, oak and climax associates on sand while the soil of the forests on clay is neutral or slightly acid (pH 6.0).

4. *Soil Temperatures*. Determinations of this factor in the course of the present study have demonstrated high extremes of surface temperatures (64° C.) in the fore-dune, poplar and pine associates on clear summer days. It appears that moderate soil temperatures are never surpassed in the oak forest; the maximum measured was 38° C. In the most perfect development of the climax forest, which was studied as found at Lakeside, Michigan, the highest surface temperature recorded was 24° C. In the spring the exposed areas of sand in the fore-dune, poplar and pine associates respond quickly to increased air temperatures and greater intensities of solar radiation. Soil temperatures in the oak and climax forests lag considerably. This lag is particularly marked in the latter community. In 1935 soil temperatures of 20° C. or above were not reached in the climax forest until July according to the records taken.

The annual minimum soil temperatures at a depth of two inches are very nearly the same for all the associates. The lowest recorded was — 3.5° C. in the poplar community. The difference between this and the simultaneous

record for the climax, -1.5°C ., is hardly of significance in the survival of the eggs of Orthoptera which occur in this latitude.

Thermograph records for August and September indicate that average soil surface temperatures in the oak forest and in well shaded sites in the poplar and pine associates are approximately equal to average air temperatures. Average temperatures at a soil depth of two to six inches are one to two degrees lower than at the surface during August and September. Surface temperatures in the climax forest average from one to five degrees lower than air temperatures for this period. The greatest deviation is on days of fairly high air temperatures and is probably greater in the early summer.

The maximum soil surface temperatures recorded in the different associates are shown in figure 1.

5. *Sunlight Intensities* were measured by O. Park ('31) by means of the McBeth illuminometer. By determination of the relative areas in full sunlight, in sunflecks and in shade, and by measurements of light intensities in each of such sites he has reduced sunlight intensities in the various associates to a standard designated by him the Ecological Light Unit. The basis of comparison is the intensity of full sunlight; light intensities in the plant communities are expressed as a per cent of full sunlight. Thus the poplar and pine communities receive about 80-90 per cent as much solar radiation at the earth's surface as do such open sites as the foredune. A marked diminution in this factor occurs in the transition from pine to oak forest; sunlight intensity on the floor of the latter associates is approximately half that in the former. Solar radiation falling on the floor of the climax forest amounts to only 5 per cent of that incident upon the foredune. The foregoing description applies, of course, only to the season extending from about May 1 to October 1.

Maximum soil temperatures show, as would be expected, a direct and rather close correlation with intensities of solar radiation.

The oak-hickory forest on clay was not considered separately by Park. The point on the sunlight axis for this associate is an approximation arrived at by a consideration of the general aspect of the sunfleck pattern of the floor as compared with those of the black oak and climax forests.

6. *Ultraviolet Radiation* was measured by photochemical and photoelectric methods in the present investigation. When the data were reduced to a standard similar to the Ecological Light Unit of Park it was found that in the case of total ultraviolet (2900-3900 Å) the diminution in intensity through the forest series is similar to that of visible light although more decided. The intensity of this radiation in the climax forest is less than one per cent that in full sunlight.

Ultraviolet of wave-length 3100 Å and shorter is apparently absent in the oak and climax forests except in sunflecks and clearings. While this spectral fraction is not indicated in figure 1 its successive diminution resembles that of total ultraviolet.

DISCUSSION

The succession of one plant associates by another effects, of course, a change in a complex of physical factors. It is entirely possible that two or even more of these are concerned in an inseparable manner in determining the local distribution of Orthoptera. There are in some instances, however, marked changes in only one factor, which, therefore, appears to be the decisive influence in the occurrence of certain species.

An inspection of table I shows that of the seven species of Orthoptera which are found on the foredune six range through the poplar and into the pine associates, while one extends only into the poplar community. The general aspect of this group of Orthoptera is distinctly western. *T. maritima interior*, however is an inland race of a species which occurs along the Atlantic coast from southern Maine to Florida. *Interior* ranges along the southern shores of the Great Lakes and along streams into Iowa and Minnesota. Both it and the typical form are confined to sandy areas near water. The other six species of the foredune have wide western ranges. Northwestern Indiana marks the eastern limits of *A. deorum*, *M. angustipennis* and *M. flavidus*. The first two of these range southwestward into Arizona and northwestward to British Columbia. *M. flavidus* reaches southern Colorado. Blatchley ('20, p. 417) says that it is known from Tucson, Arizona.

S. collare, *P. fenestralis* and *M. mexicanus* range extensively east, west and south of northern Illinois. *M. mexicanus* is reported as much more abundant in the western part of its area of distribution.

Reference to figure 1 will show that the foredune and poplar associates are much alike in their physical factors. There is only a slight modification of light and ultraviolet intensities. The soil pH in the poplar associates approaches neutrality from the slightly alkaline condition of the foredune. No actual measurements of evaporation and soil moisture on the foredune have been made but these factors are certainly not less than in the poplar associates. From Fuller's discussion of the effect of vegetation on soil moisture one would expect more available water on the foredune than in the poplar community. With this similarity of environment we find (table I) seven species of Orthoptera common to the two associates and none peculiar to either.

The transition from poplar to pine associates is marked by a decrease in soil moisture; soil water in the pine community amounts to only half that in the poplar due, probably, to the demands of the abundant vegetation. There is a decided decrease in the rate of evaporation as determined by Fuller. The vegetation of the pine dune is quite different from that of the first two associates discussed. This difference, in Fuller's opinion, is best correlated with diminished evaporation. The other physical factors undergo little modification in the transition from poplar to pine community.

Of the species of Orthoptera present in the first two communities one only, *T. maritima interior*, is absent from the pine dune. Its local distribu-

tion appears best correlated with soil water. Its geographical range also suggests a dependence upon the amount of soil moisture as it is restricted to sand areas near water east of the ninety-fifth meridian. The other species, with the exceptions of *S. collare* and *M. mexicanus*, are, in the Chicago area at least, peculiar to sand. Their limitation to this type of soil is probably a phenomenon depending upon the more constant and always moderate supply of soil water in sand as contrasted to clay soils (Fuller, '14, p. 227). The exclusion of *interior* from the pine dune community would be interpreted, according to this hypothesis, as due to a greater minimum requirement in this respect than is the case with the other species. If we assume the validity of this suggestion the critical point would be the selection of sites for oviposition or the early development of the eggs or both, since it is only in the summer and early autumn that soil water is deficient in the pine associates.

M. mexicanus is an abundant species on the high prairie of the moraine region *S. collare* has also been found on clay hills where there is some sand mixed with the glacial till, as along the fossil shoreline near Smith, Indiana. Unshaded and well drained clay soil in this region is characterized by great extremes of soil water; the moisture content is very high during winter and spring while pronounced desiccation takes place in the summer. The tolerance of these two species for both extremes of soil moisture locally is also suggested by their extensive distribution. Both range from the Atlantic states to Utah and Arizona.

The succession of the pines by the black oaks brings about little change in soil moisture, soil pH and evaporation (fig. 1). The most radical changes in the physical factors occur in the cases of light, ultraviolet and maximum soil temperatures.

From table I it is apparent that the transition from pine to oak forest marks an important zone of tension in the succession of Orthoptera. Of the twenty-three species listed from the black oak forest only five occur in the pine associates and these are of sporadic appearance. On the other hand, of the thirty-one species found in the oak-hickory forest on clay, which differs markedly from the black oak forest on sand only in the matter of soil water, twenty-two or 71 per cent are also to be found in the black oak forest on sand.

The change in the characteristic species of Orthoptera in the transition from pine to black oak forest is best correlated with sunlight intensities and soil temperatures. The correlation with ultraviolet intensities is, judged from experiments made in the course of this study, superficial only. No basic importance to Orthoptera of this radiation has been demonstrated. The correlation with light intensities is very likely not due to its visual effect. Observations in the forest show a concentration of nymphs of Orthoptera around the margins of clearings and in sunflecks, especially in May. This fact was noted by Shelford ('13, p. 241). It has been observed that nymphs of *A. testaceus* and *M. viridipes* which were in a clearing exposed to full

solar radiation retired to shaded sites when soil surface temperatures rose to 35° C. The nymphs of *A. testaceus* often crawled beneath the mat of leaves on the ground. Since this behavior took place about an hour later than the incidence of daily maximum sunlight intensities (11:45 C.S.T.) it appears to have been a reaction to heat rather than to light as illumination. The increased rate of evaporation with higher soil temperatures has not been determined; possibly this factor exercises an important influence in the behavior described. Again, there is a migration of *A. sulphurea* from the pine into the oak forest in late May. From Fuller's data ('14, p. 201, 202) it appears that the rate of evaporation in the two associates is not greatly different at this time. His determinations, however, were not extended to the more open parts of the pine community. Since soil surface temperatures in such exposed sites are known to surpass 50° C. in late May, evaporation in the air immediately above the sand must be greatly increased. This condition prevails over three-fourths or more of the pine associates; areas of moderate soil surface temperatures are limited to small, heavily shaded spots almost or quite devoid of herbaceous vegetation and unsuited to the existence of Orthoptera.

The suggestion that sunlight is not of greatest importance because of its visual effect is substantiated by the experiments of Langford ('30), who found no difference in the growth rate of nymphs of *M. bivittatus* in darkness and in light when temperatures were maintained at a predetermined optimum. Since the species used lives naturally in environments where it is exposed to high intensities of sunlight this experiment must be considered as having definite bearing on the rôle of sunlight in the ecology of Orthoptera. Temperature was not adequately considered in the experiments of Nabours, Larson and Hartwig ('33) and of Sabrosky, Larson and Nabours ('33), who reported a positive effect of light on the growth of grasshoppers.

The abrupt dropping out of the species found in the preceding associates is also best correlated with diminished sunlight intensities and lower soil temperatures. Soil temperatures in the oak forest lag behind those of open sites in the annual rise in April and May. It is entirely possible that the higher soil temperatures prevailing at this season in the earlier associates may be essential to the development of the Orthoptera which are confined to these communities. The direct utilization of radiant energy as heat by the growing nymphs may also be of significance. Such an assumption seems to explain best the results of the experiments of Sabrosky, Larson and Nabours which have been cited.

Graham ('20) has showed that the temperature of logs exposed to direct sunlight may rise above 50° C. on summer days. Such temperatures would act upon the eggs of such species as *Chloealtis conspersa*, *M. walshii* and the species of *Parcoblatta*, which use logs as sites of oviposition. That such is the case is indicated by the finding of numbers of unhatched and shriveled oothecae of *P. pennsylvanica* under the bark of pine logs. Graham consid-

ered the high temperatures of such habitats the most important factor in conditioning the fauna.

The oak-hickory forest on clay as exemplified at Palos Park, Illinois, is not greatly dissimilar to the oak forests on sand in respect to its fauna of Orthoptera. As pointed out before, these two associates have twenty species in common with one species confined to the oak forest on sand while ten species which occur in the oak forest on clay have not been taken in the similar forest on sand. In the case of such nocturnal species as *A. oblongifolia* this may be the result of oversight as night collecting has not been done in the dunes and these insects, where they occur, are not much in evidence during the day. The use of molasses traps for *Ceuthophilus* in the dunes has been wholly unproductive. A few nymphs of some species of this genus were found in a black oak forest on sand at Saugatuck, Michigan.

The only marked change in the physical factors from the black oak to the oak-hickory forest (fig. 1) is in the matter of soil moisture. Hence this is suggested as the factor the increase of which allows the advent of such Orthoptera as *Ceuthophilus*, *M. viridipes*, *M. gracilis* and *A. testaceus*. That the occurrence of these is not due to the fundamental properties of clay is shown by their establishment in the climax forest on sand at Saugatuck, Michigan, and, in the case of *M. viridipes*, its presence in the subclimax on sand at Lakeside, Michigan.

Where clearings are present in the climax forest several species of Orthoptera which also occur in the preceding associates have been taken. To these are added four species which, insofar as the series of habitats under discussion is concerned, are characteristic of the climax forest only. The beech-maple forest at Lakeside, Michigan, presents an almost unbroken leaf canopy, very low sunlight intensities in summer and low maximum soil temperatures. Here the number of species of Orthoptera is greatly reduced. Four species of *Ceuthophilus* have been found under logs and the katydid *Pterophylla* has been heard in the trees.

The low sunlight intensities and low soil temperatures in this type of habitat appear to be decisive factors in the limitation of the fauna of Orthoptera. Evaporation is 25 per cent less than in the oak-hickory forest and averages only 7 cc. per day during the summer. While Hamilton ('36) has demonstrated that too great humidity is detrimental to some locusts one can make no suggestion as to the effect of atmospheric moisture in the climax forest. Parker ('30) gives 17° C. as the temperature threshold of *M. mexicanus* eggs. Such soil temperatures have not been recorded in the climax forest until late June and July in the measurements made in the course of this study, which suggests that this factor is an important one in the exclusion of many species of Orthoptera. On the other hand the restriction of the low vegetation of the forest floor to *Galium* could well be the decisive influence.

Little attention has been directed to soil pH in the foregoing discussion. While the author is not aware of any experimental work on the effect of this

factor on the eggs of Orthoptera, investigation of the effect of relatively narrow ranges of pH on animals has produced, in general, negative results. Even in the case of such organisms as earthworms, which live in very intimate association with the soil, Allee, Torvik *et al.* ('30) conclude that a range of pH 6.0–8.0, which is that dealt with at present, is not of direct significance in influencing distribution.

Considerable attention has been directed by field orthopterists to the vegetation with which certain species are often associated. While it is possible to define a very good correlation in a limited area, experimental evidence indicates a very wide latitude in the food requirements of all the species which have been reared under laboratory conditions. There are, undoubtedly, some plants upon which Orthoptera will not thrive (Carothers, '23) but such plants as can be used as food for one species are equally useful for others. As Morse ('99, p. 315) says, their food requirements are "... general in character rather than special, a question of quantity rather than quality." In this laboratory *M. differentialis*, *M. viridipes*, *A. sulphurea* and *A. testaceus* have been reared on lettuce and alfalfa hay, *Poa* and various other grasses. Adults of *T. maritima interior* and *M. fasciatus* have fed freely on maize leaves, lettuce and wheat sprouts and have mated and oviposited while on this diet. *M. punctulatus* nymphs taken from beech and maple trees were reared to maturity on the leaves of elm. This species has been observed feeding on the tamarack and cassandra (*Chamaedaphne*). In the light of such evidence it does not seem probable that the occurrence of certain Orthoptera is strictly dependent upon particular plants. Moreover the distribution of some species of Orthoptera is much more restricted than that of the plants with which they are often found. The converse of this is equally and, in the case of destructive species, forcibly true.

There appears to be no lack as to the quantity of plant material available for food in any of the communities described unless it be in the climax forest. The most primitive community, the beach, is practically bare of plants. While no actual data have been taken on the relative quantities of herbaceous vegetation the rather abundant growths of grasses in the earlier associates are not perceptibly affected by the feeding of the grasshoppers found there.

It seems, from the results of this study, that the controlling factors in the local distribution of the Orthoptera of the Chicago area are sunlight, as heat, and soil moisture. This conclusion is similar to that arrived at by Dreyer and T. Park ('32) in a study of the factors determining the situation of the nests of *Formica ulkei* Emery. Talbot ('34, p. 419) cites instances of the effect of soil temperature on the behavior of ants. Chapman, Mickel and Parker ('26) found that confinement to sand at 55° C. for one minute was sufficient to kill *Gryllus assimilis*. *Spharagemon aequale* (collare, Hebard, '32, p. 30) was able to survive for much longer periods, even with its wings clipped, by extending its legs and thus raising its body from the hot sand. They also found, in laboratory experiments, that the crickets died at a tem-

perature of 49° C. with paralysis beginning at 42° C. The grasshopper *Spharagemon*, which inhabits open situations in the dunes, died at 55° C. with paralysis beginning at 50° C.

It is improbable that evaporation has no effect in the distribution of Orthoptera. The only experiments relating to this factor have been performed using relative humidity as the index to moisture conditions in the atmosphere. Hamilton ('36), using two species of African locusts, found rather wide latitudes of this factor tolerated. At temperatures of 80–90° F. *Locusta migratoria* developed at R.H. 35–85 per cent. *Shistocerca gregaria* was less tolerant in this respect, developing only at R.H. 45–75 per cent. The absence of absolute meaning in relative humidity makes impossible any close comparison of experiments using this factor with natural conditions studied by means of evaporimeters.

A comparison of Talbot's ('34) experiments on ants with those of Chapman, Mickel and Parker ('26) on insects of various orders suggests high soil temperatures as a more effective and more rapidly acting lethal factor than is evaporation as indicated by relative humidity. Whereas in Talbot's experiments ($T=41^{\circ}\text{C.}$; $\text{R.H.}=8\%$) individuals of the least resistant ant species survived for fifty minutes, in the experience of the latter workers a few minutes at 50–55° C. were sufficient to kill those insects not adapted in some manner to the high surface temperatures of sand. Mosauer ('36) found that desert reptiles died within nine minutes when confined to sand at a temperature of 55–60° C. The critical body temperature was between 40° and 45° C. While these last experiments used animals entirely different from those under consideration they serve to illustrate the effectiveness and rapidity of action of high soil temperatures in restricting the range or, in some instances, the time of activity of animals. In the case of insects evaporation produced by these high temperatures must play some part. One could demonstrate, probably, a differential susceptibility to this factor in species of Orthoptera from different habitats as did Talbot with ants.

The restriction of certain species of Orthoptera to sand in this area appears to be a phenomenon dependent upon the fairly constant supply of water in this type of soil and the absence of either extreme of soil moisture. Fuller ('14) has demonstrated the difference in this respect between sand and clay soil in the region about Chicago. In the entire complex of Orthoptera found in this area no species is restricted to clay soil while thirteen species are confined, apparently, to sandy soil. Since the same or closely related species of plants are to be found on both types of soil and other factors such as sunlight and evaporation are similar in habitats of equal exposure, soil moisture seems clearly to be the controlling influence in determining the orthopteran fauna of sand as contrasted to clay.

There appear to be very local influences, particularly in the oak-hickory forest on clay, which effect a differential distribution of the species within the area covered by one associates. The topography of the land suggests soil

water as affected by drainage as the main factor operative. Thus in the forest of this type most studied *M. viridipes* and *A. testaceus* are most abundant on the sides of a broad, gently sloping ravine while *M. fasciatus* and *M. keeleri luridus* are almost wholly restricted to the high parts of the forest. If we assume, as is likely, that the soil of the ravine has a greater moisture content than has that of the more elevated portion of the forest the very local distribution of these species corresponds to their occurrence in the associates considered. The first two are absent from the oak forest on sand, where soil moisture is small in amount, while the latter two are to be found in such habitats. *Luridus* especially is characteristic of the oak forest on sand. That their local distribution depends in large measure on differences in soil moisture is substantiated by their geographic ranges; the Mississippi River marks the approximate western extension of *M. viridipes* and *A. testaceus*; *M. fasciatus* and *M. luridus* range westward to and beyond the one hundredth meridian.

Morse ('04) offered a classification of locust societies based upon a primary division into geophilous and phytophilous groups. Each of these he further separated into campestrian and sylvan assemblages of species. The designations of these and of the lesser groupings suggested, saxicolous, arenicolous, humicolous, are descriptive of the gross features of the habitats. While in a general descriptive way Morse's classification is entirely valid my own experience is in accord with that of Shull ('11), who noted that conditions of a very local nature were often of great importance, a fact not overlooked, however, by Morse.

TABLE II. Schematization of the communities of Orthoptera as suggested by their distribution in the Chicago area compared to the arrangement of the plant communities as recognized by botanists

Orthopteran community	Plant community ³
(A) <i>Spharagemon collare</i>	Foredune, Poplar, Pine
(1) <i>S. collare</i> - <i>T. m. interior</i>	Foredune, Poplar
(2) <i>S. collare</i> - <i>M. angustipennis</i>	Pine
(B) <i>Parcoblatta pennsylvanica</i>	Black oak, Oak-hickory, Subclimax on sand, Climax
(1) <i>P. pennsylv.</i> - <i>M. k. luridus</i>	Black oak, Oak-hickory in part
(2) <i>P. pennsylv.</i> - <i>M. viridipes</i>	Oak-hickory, Subclimax on sand, Climax in part
(3) <i>P. pennsylv.</i> - <i>Ceuthophilus</i>	Oak-hickory in part, Sub- climax on sand, Climax

³ Cowles, '01.

It is evident (table I) that the ecological distribution of Orthoptera in the Chicago region is not indicated in an absolute manner by the dominant plants of the associates considered. When these insects alone are considered they appear to be grouped into two major assemblages of species, which we may designate the *Spharagemon collare* and the *Parcoblatta pennsylvanica* com-

munities. The first of these corresponds to the foredune, poplar and pine associates of plant ecologists, the second to the black oak, oak-hickory, subclimax on sand and climax associates. Solar radiation intensities seemingly serve as the best indices of these primary divisions.

There are two aspects of the *S. collare* assemblage, one of which is indicated by the presence of *T. maritima interior* but which also includes all the other species. This we may call the *collare-interior* community. The other, characterized by the great abundance of *M. angustipennis*, is aptly described as the *collare-angustipennis* community. The division in the major *collare* group is brought about by differences in soil water as judged by the data available.

The other primary assemblage of species occurs in three intergrading aspects. We may designate the secondary groups the *P. pennsylvanica*-*M. k. luridus*, the *P. pennsylvanica*-*M. viridipes* and the *P. pennsylvanica*-*Ceuthophilus* communities. As is apparent in table II the groupings suggested here do not coincide with the associates as schematized by plant ecologists.

The delimitation of the first two of the secondary groups of the *P. pennsylvanica* assemblage (insofar as it exists) appears again to be an effect produced by differences in soil water. Suggestion as to the specific factor or factors operative in the segregation of the *M. viridipes* and *Ceuthophilus* communities is not so readily made although sunlight intensities and resultant temperatures are indicated.

SUMMARY

The physiographical and vegetational features of the plant succession on sand and of two types of forest on clay in the Chicago region are reviewed.

Quantitative determinations of the physical factors operative in these associates are also reviewed.

The species of Orthoptera characteristic of these associates are listed and discussed.

It is concluded that the change in the typical species of Orthoptera from foredune to pine associates is dependent upon decreasing soil moisture.

Sunlight intensity appears to be the principal factor operative in the faunal change from pine to black oak associates. Its action is apparently as heat rather than as illumination.

The greatest number of species of Orthoptera is found in the oak-hickory forest on clay. This is correlated with an abundant soil moisture, a middle range of light intensities and moderate soil temperatures.

The greatly reduced number of Orthoptera in the climax forest may be due to low soil temperatures or to lack of variety of herbaceous vegetation.

The restriction of certain species to sand may be accounted for on the basis of a requirement of soil moisture of more constant amount and of lesser extremes than is the condition in clay soil.

Two major communities of Orthoptera are recognized among the species

dealt with. One of these is divided into two, the other into three lesser groups.

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